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# HOMING ABILITY OF BREEDING MALE TREE SWALLOWS

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Abstract.—We inadvertently examined homing ability in Tree Swallows (*Tachycineta bicolor*) when we removed twelve males from their nestboxes in 1993 as part of another study. These males were removed just prior to their mate's fertile period and released either 125 or 250 km away. Six of them were documented as having returned to the study area that same season. Three of these males subsequently nested successfully, with two breeding in their original nestbox with their original mate. Another three males returned to the study site the following year. Tree swallows have excellent homing ability, and are strongly motivated to return to their breeding site. They appear to navigate because one of the homing males was released north of the study site in what was most likely an unfamiliar area.

**HABILIDAD PARA ENCONTRAR SU HOGAR POR PARTE DE MACHOS REPRODUCTIVOS DE *TACHYCINETA BICOLOR***

Sinopsis.—Inadvertidamente, examinamos la habilidad de machos reproductivos de *Tachycineta bicolor* para encontrar su hogar cuando removimos a 12 individuos de sus nidos en el 1993. Estos individuos fueron removidos de sus nidos en el periodo previo a que sus parejas cayeran en el periodo fértil y movidos de sus áreas entre 125 y 250 km. Seis de éstos regresaron al lugar en donde fueron capturados la misma temporada. Tres de éstos anidaron exitosamente. De éstos, dos utilizaron la misma caja en donde fueron capturados y se aparearon a la misma hembra. Otros tres machos regresaron al área el próximo año. La especie mencionada tiene una gran habilidad para encontrar el lugar en donde viven y están altamente motivadas a regresar al lugar en donde se reproducen. Estos parecen navegar, debido a que uno de los machos fue liberado al norte del área donde fue capturado en un lugar poco familiar para éste.

Avian homing ability has been the subject of hundreds of studies and is particularly well documented in the homing pigeon (*Columba livia*) (reviewed in Able 1995, Schmidt-Koenig and Keeton 1978). From extensive bird-banding studies, we know that many migratory species possess some homing ability because they exhibit strong site fidelity between years (Harvey et al. 1979, Jakobsson 1988, Regosin and Pruett-Jones 1995, Shields 1984, Thompson et al. 1994, Weatherhead 1995). Homing ability can also be estimated by examining the propensity of an individual to return to its breeding site within a season. Several researchers have removed males and females from their nest sites and transported them to another location for release (Able et al. 1984, Dall'Antonia et al. 1995, Ioale et al. 1994, Nastase 1982, Pärt 1995, Sargent 1962, Southern 1959). Results vary. Some species were released close to their breeding site and did not have the expected high homing success. Wood Thrushes (*Hylocichla mustelina*), despite being released close to their nests (6.5–17.3 km away), had a homing success of 43% (Able et al. 1984). Similarly, Collared Flycatchers (*Ficedula albicollis*) were released close to their nestboxes (1.5–6 km away), and only 54% returned (Pärt 1995). Homing pigeons, however, had 100% homing success after being released 4–103 km from their loft (Ioale et al. 1994). Species from the Hirundinidae such as Barn

Swallows (*Hirundo rustica*), Bank Swallows (*Riparia riparia*), Northern Rough-winged Swallows (*Stelgidopteryx serripennis*), and Purple Martins (*Progne subis*) are excellent homers, even over long distances (Nastase 1982, Sargent 1962, Gillespie 1934 *in* Sargent 1962, Southern 1959, respectively). Until now, however, no information existed on the homing proficiencies of Tree Swallows (*Tachycineta bicolor*).

We inadvertently conducted a homing experiment on a population of Tree Swallows when we removed and displaced males from their nestboxes as part of another study in which we examined the mating success of females paired with replacement males.

## METHODS

In early May of 1993, we removed twelve male Tree Swallows who were breeding in nestboxes at the Queen's University Biological Station (44°34'N, 76°19'W) in southeastern Ontario. These twelve males had been among the earliest settlers on the study site, obtaining nestboxes between 6–8 April. They paired successfully with females and defended their nestboxes until the time of their removal (between 6–10 May). All males had been banded and individually marked with acrylic paint for identification. Eleven of these males were driven southwest to Toronto, Canada, a distance of 250 km, where they were released. The twelfth male was driven northeast and released in Ottawa, Canada, a distance of 125 km. All males were caged and transported by car to their release sites during the daylight hours. They were released in the late afternoon, or early evening on the same day as their removal from the nestboxes.

DNA fingerprinting was done on blood collected from the families of the three males who successfully returned and nested that season, following the procedures outlined in Lifjeld et al. (1993) and Barber et al. (1996). Male age was tested for normality using a Shapiro-Wilk W test; a two-tailed Mann-Whitney test corrected for ties was used. All ages reported (except for three) indicate minimum age as determined by number of years of breeding experience on the study sites.

## RESULTS

Of the twelve males, six (50%) were subsequently observed in the study site within the same breeding season (Table 1). In the following year (1994), four of the removed males (33.3%), one of which had homed successfully in 1993, returned to breed in the study area. Therefore, nine of the twelve removed males were resighted within a year at the study site, suggesting that their viability was unaffected by the removal experiment.

The six males who homed successfully within the month were not significantly older than the males who did not return to the study site that year ($\bar{x} \pm SE = 3.3 \pm 0.67$ years vs. $2.0 \pm 0.68$; Mann-Whitney U: $U = 9.5$, $n = 6, 6$, $P = 0.15$). Similarly, males who homed were no more familiar with the study area than males who did not home (two-tailed Fisher's Exact test: $n = 12$, $P = 0.24$), although the trend was in the expected direction; 5/6 homing males had nested within the study site

TABLE 1. A description of the six male Tree Swallows returning to the study site within a month of their removal. Males A–E were released in Toronto; Male F was released in Ottawa.

| Male | Released | Returned by | Years at site | Comments |
|---|---|---|---|---|
| A | 6 May | 29 May | 1 | He perched momentarily on a nestbox within the study area, but never nested. |
| B | 7 May | 16 May | 3 | A replacement male settled on 7 May with resident female and they remained paired for the season. On 16 May, Male B was seen at another nestbox 120 m away from his original one. Male B paired with new female (her mate disappeared), and they fledged five nestlings (from six eggs) of which four nestlings were extra-pair young. |
| C | 8 May | 12 May | 4 | A replacement male settled with the resident female on 8 May. Male C returned and regained nestbox and mate; replacement male never again observed. Two nestlings fledged (from six eggs). Fingerprinted four nestlings; three were extra-pair young, but were not sired by replacement male. |
| D | 8 May | 15 May | 5 | Was sitting under his original nestbox, unable to fly, but without visible wounds at 0500 h on 15 May. Resident female and replacement male were on the nestbox. Male D died the following day in the lab. |
| E | 8 May | 26 May | 5 | Observed on a nestbox within the study site (also seen on 19 and 23 June). Never nested. |
| F | 10 May | 12 May | 2 | Returned to original female at original nestbox by 0530 h on 12 May. She began nest-building. In his absence, several replacement males tried unsuccessfully to settle with her. All six nestlings fledged (all were sired by Male F). |

in previous years, while only 2/6 nonhoming males had done so. Removed males who returned but did not regain their nestbox (males A, B, D and E in Table 1) did not sire any of the offspring in their original mate's brood. All extra-pair young were genetically related to the resident female, but not the male, and were therefore not a result of intraspecific brood parasitism.

## DISCUSSION

Our results indicate that at least half of the Tree Swallows that we displaced from their nest site were able to return. Because the population of Tree Swallows that we study migrates north to the breeding grounds from places such as the southern U.S., the Caribbean, and Central America (Butler 1988, Robertson et al. 1992), the male who was released in Ottawa, north of the study site, had likely never before encountered the area. This male was 2-yr old, having hatched in the same study site to which he returned to breed. He appeared to be truly navigating because he flew from an unfamiliar place in a southerly direction that was most likely unusual at that time of the year (Griffin 1955). It is also likely that the males released in Toronto, west of the study site, were unfamiliar with that area.

Other species in the family Hirundinidae home over a long distance with a speed that suggests true navigation, and not random searching (Griffin 1955, but see Sargent 1962). Given the excellent homing ability of other swallow species (Gillespie 1934 *in* Sargent 1962, Matthews 1955 *in* Sargent 1962, Nastase 1982, Ruppel 1934, 1936, 1937 *in* Nastase 1982, Sargent 1962, Southern 1959, Wojtusiak and Ferens 1947 *in* Nastase 1982), it is not surprising that Tree Swallows, members of the Hirundinidae, also possess excellent homing abilities. Aside from their ability to navigate back to the nesting site within a season, Tree Swallows typically have a high level of site fidelity between years. In two studies, 40% (Chapman 1955) and 60% (De Steven 1980) of Tree Swallows returned to breed the following year. Their intense site fidelity suggests that a high value is placed on known nest sites. Tree Swallows are secondary cavity-nesters and as such their breeding opportunities are limited by the availability of excavated cavities (Robertson et al. 1992). There are not enough cavities for all members of the population; floaters are prevalent (Stutchbury and Robertson 1987). Our results confirm the abundance of floaters in the population since other males were quick to fill the nestbox vacancies left by the removed males (Barber 1997). Given the limited availability of these nesting cavities, and the intense competition for them, a high fitness value may be attached to nest sites where males have been able, in the past, to establish a territory, resulting in a strong motivation to return to it.

In some passerine species, site fidelity to the breeding grounds is age- (Lemon et al. 1996, Pärt 1995) or sex-dependent (Lemon et al. 1996, Murphy 1996, Pärt 1995, Shields 1984), but this does not appear to hold true for Tree Swallows. In this study, age differences between homing and nonhoming males were nonsignificant. In two other Tree Swallow studies, DeSteven (1980) found no significant differences in site fidelity between female yearlings and older females, and Chapman (1955) found no differences in return rates between males and females.

Another potential selective factor affecting site fidelity is that individuals become familiar with each other. Neighbor familiarity has been observed in Red-winged Blackbirds (*Agelaius phoeniceus*) (Beletsky and Orians 1989, Weatherhead 1995). Prior knowledge of the breeding males and females in an area could provide Tree Swallows with important information about the quality of their neighbors. This information could have significant implications for female mate choice when choosing both within-pair and extra-pair mates.

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